AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY 107:87–96 (1998)

Canine Tip Wear in Male and Female Anthropoids

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KEY WORDS Canine teeth; sexual dimorphism; anthropoids; dual selection hypothesis

ABSTRACT One component of the "dual selection hypothesis" (Greenfield [1992a] Year. Phys. Anthropol. *35:*153–185) is that the tips of female canines are commonly blunted and more frequently so than those of conspecific males. Data derived from two randomly selected age-graded samples of *Macaca fascicularis* (n = 70) and *Colobus badius* (n = 59) show that at least 80% of the females exhibit tip blunting on one or both canines and that frequencies of blunting are far greater than those of conspecific males in both jaws. Sexual dimorphism in mandibular canine morphology and wear and other recently critiqued aspects of the "dual selection hypothesis" (Plavcan and Kelley [1996] Am. J. Phys. Anthropol. 99:379–387.) are also discussed. Am J Phys Anthropol 107:87–97.

INTRODUCTION

According to the "dual selection hypothesis" (Greenfield, 1992a), two forms of selection affect canine size and form in most anthropoids: incisal selection and weapon selection. One piece of evidence presented in support of the assertion that incisal selection exists was that canine tip wear is common in females and that it occurs more frequently than in conspecific males. Because this appeared to be as consistent as dimorphism in canine size and morphology, no formal data showing this phenomenon were collected.

Recently, Plavcan and Kelley (1996) critiqued this and other components of the "dual selection hypothesis." In their critique, they presented data suggesting that tip blunting was not common in females and that frequencies of wear were not dimorphic. Unfortunately, the data they presented were derived from small intraspecific samples that were not age-graded. Tip-blunting and canine wear, in general, are age-related phenomena. Younger adults have little or no tip blunting in either sex and sexual differences generally emerge with increasing age. Thus, proper quantification of this age-related phenomenon requires observation of a large number of age-graded individuals in each taxon. Since none of the samples used by Plavcan and Kelley (1996) were large and none were age-graded, their data are not appropriate for testing the original assertions (Greenfield, 1992a).

In this article, age-graded canine wear data from two large samples are presented, along with a response to a variety of points raised by Plavcan and Kelley (1996) about the dual selection hypothesis. This response covers three major issues. One of these concerns the function of the mesial cristid, i.e., whether this dental feature is only a simple and nonfunctional allometric phenomenon related to canine size or whether its occlusion with the distal portion of I^2 represents a functional contribution to incisal occlusion. The second issue concerns the overlap in form and function between incisors and canines and the conclusion that early human canines, like modern human canines, were used as incisors. The third

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Received 20 November 1996; accepted 31 May 1998.

*TABLE 1. Canine tip blunting**

Age group →	0	1	2	3	4	% of total
Maxillary canines						
M. fascicularis males (n = 41)						
No. tip blunted	0	0	1	2	0	7.3
No. not tip blunted	3	19	8	6	2	92.7
M. fascicularis females (n = 29)						
No. tip blunted	2	5	2.5	1.5	0	37.9
No. not tip blunted	8	3	2.5	3.5	1	62.1
C. badius males (n = 33)						
No. tip blunted	0	0	0	2	0.5	7.6
No. not tip blunted	2	7	8	8	5	92.4
C. badius females (n = 26)						
No. tip blunted	0	5.5	2.5	0.5	1	36.5
No. not tip blunted	3	5.5	4.5	1.5	2	63.5
Mandibular canines						
M. fascicularis males (n = 40)						
No. tip blunted	0.5	4	2.5	5.5	1	33.8
No. not tip blunted	2.5	13.5	6.5	2.5	1	66.2
M. fascicularis females (n = 31)						
No. tip blunted	7.5	7	5	4.5	1	80.6
No. not tip blunted	4.5	1	0	0.5	0	19.4
C. badius males (n = 31)						
No. tip blunted	0	1	2	5.5	3	37.1
No. not tip blunted	2	5	6	4.5	2	62.9
C. badius females (n = 25)						
No. tip blunted	1	6	7.5	2	3	78.0
No. not tip blunted	2	3	0.5	0	0	22.0

* Specimens with bilateral asymmetry of tip blunting were scored as 0.5.

issue concerns the significance of deciduous canine size, form, and function in anthropoids, and the wide range of phenotypic expression found among the three forms and sizes of canines in virtually all anthropoid species.

MATERIALS AND METHODS

Wild-caught specimens of two randomly selected (aside from large sample size) taxa were examined at the Mammalogy Department of the American Museum of Natural History; *Macaca fascicularis* and *Colobus badius*. These samples (n = 70 and 59, respectively) were age-graded into five subsets (0, 1, 2, 3, and 4) by wear on M_3: 0 (no wear), 1 (tips of cusps show very slight wear), 2 (cusps half worn away), 3 (cusps worn flat), and 4 (very advanced wear).

Specimens were counted as having tip blunting wear only when the plane of tip wear was flat, or nearly so, and was clearly not an extension of wear from the mesial and distal edges that had reached the apex of the crown. In most of the observed cases of tip blunting, microscopic striations, pitting, and scratches on the blunted surface were oriented in different directions from similar wear features on the distal and mesial edges. This also indicated that the observed tip blunting was not an extension of mesial and distal edge wear. No attempt was made to quantitatively assess causes of tip blunting (puncture crushing, occlusion with the other canine, or occlusion with the lateral incisor). All forms of wear noted below were observed with a stereoscopic microscope set at a magnification of 15×.

RESULTS

The age-graded samples for both taxa (Table 1) show that female C^1s are far more frequently tip blunted than male C^1s. Frequencies of female C^1 blunting reported here are higher than those reported by Plavcan and Kelley (1996) (although the differences could be simply related to differences in the age-grade composition of the samples). As predicted, younger adult specimens exhibit less frequent tip blunting than older individuals. In addition, in both taxa, tip blunting of female C_1s (Table 1) was more frequent than for their C^1s and far more frequent than on conspecific male C_1s. These data show that at least 80% of all females exhibit tip blunting on one or both canines. I

consider these data appropriate and consistent with the assertion that tip blunting is common in female anthropoids and that it occurs at a much higher rate in this sex in both jaws.

While blunting wear was not quantified into categories of causes, Greenfield (1992a) concluded, as a consequence of occluding both jaws, that C_1 tip blunting in females was primarily a consequence of an interaction with the distal moiety of I^2 and, less often, interaction with C^1. In comparison, C^1 tip blunting seemed to be a roughly equal consequence of tip-to-tip occlusion with C_1 and puncture crushing. In this respect, I agree with Plavcan and Kelley that C^1/C_1 tip-to-tip blunting is not as frequent as I had suggested earlier. This is of no importance, however, as far as the "dual selection hypothesis" is concerned because tip-to-tip wear and puncture crushing are both uses that favor short crowns that wear apically, both occur commonly in anthropoids, and both could have contributed to the selection leading to canine reduction in hominids when selection related to their use as weapons was eliminated.

One other aspect of crown wear noted was that all forms of wear (tip-to-tip blunting, mesial and distal edge wear, and puncture crushing) resulted in the loss of canine projection in most females by age group 2 or 3. This shows that for most of their adult lives females have canines that are little more effective as weapons than any of the other teeth. That Plavcan and Kelley (1996) can cite only one species where females are known to use their canines to inflict wounds shows that this is an exception that supports the rule that female anthropoids generally do not use their canines as weapons. Other exceptions can be expected in taxa where female canines are large like those of conspecific males (for example, *Hylobates*). The sociobiological reasons why females should not engage in this type of physically dangerous aggression have already been identified by others (Dunbar, 1988).

That adult unworn female canines are much shorter than those of conspecific males (and could not, for this reason, be functionally equivalent to male canines) cannot be explained as a consequence of less intense weapon selection ("less selective pressure") operating on their canines. Less intense selection results in increased genetic and phenotypic variation, not necessarily much smaller size. In fact, across all anthropoids, female canines consistently exhibit *less* variation than conspecific male canines (Swindler, 1976), falsifying Plavcan's and Kelley's "selection pressure" hypothesis. No selection for weapon use in most taxa, incisal usage (and perhaps, for the maxillary canine, selection for puncture crushing as well as incisal selection), and correlated response (Greenfield, 1996b) currently is the only viable explanation.

DISCUSSION

The mesial cristid

Another important aspect of morphology supporting the assertion that female and deciduous mandibular canines are used as incisors is the mesial cristid. Is the mesial cristid an incisal adaptation or is it a simple allometric phenomenon related only to canine size, as Plavcan and Kelley (1996) have suggested? While male (large), female (medium), and deciduous (small) canines appear to be morphological distortions of each other (particularly in relation to their ontogenetic development), there is a variety of evidence (noted below) to show that these distortions, like those cited by D'Arcy Thompson (1917), are a function of different natural selection pressures rather than outcomes of a simple allometric growth trajectory.

Six observations bear on this matter. First, while the size of the mesial cristid is significantly associated with crown height in females (Greenfield, 1993), regressions indicate that for all taxa the independent variable explains only 52% of the variance. Thus, for example, according to Plavcan's and Kelley's hypothesis, one would predict large mesial cristids on the female canines of *Gorilla, Pan,* and *Alouatta.* Female canines in these genera are small compared to females of other closely related genera and much smaller than those of conspecific males. However, mesial cristids are poorly developed on female canines in all three genera

and nearly as poorly developed as in conspecific males (Greenfield, 1993). Second, some variation in mesial cristid development is clearly associated with heritage rather than canine height or projection—females of taxa from different phylogenetic groups have comparable sized canines but consistently different degrees of mesial cristid development (ceboids vs. cercopithecoids); and taxa from the same phylogenetic group have similar sized mesial cristids but varying canine heights and projections relative to body size (cercopithecoids) (Greenfield, 1993). Third, some mesial cristid variation is associated with diet. Females of folivorous species tend to have smaller canines but also smaller, not larger, mesial cristids. This is consistent with incisal usage, as folivores tend to have relatively smaller incisors and less incisal preparation of food than frugivorous species (Hylander, 1975). Fourth, *intraspecies variation* in male canine height is marked (in fact, coefficients of variation are higher for male canine measurements than they are for measurements of any other tooth (Swindler, 1976; Gingerich and Schoeninger, 1979)) but there is no corresponding variation in male mesial cristids. Fifth, there is a much greater magnitude of *interspecies variation* in male anthropoid canine projection, height, and shape but there is no significant covariance of male mesial cristids[1] with any of these quantitative measures of canines (Greenfield, 1993). Sixth, in a regression of mesial cristid size on deciduous mandibular canine height in 40 taxa (this author's unpublished data), although the variables were significantly associated, only 38% of the variance in mesial cristid size was explained by the independent variable. Similarly, mesial cristid size regressed on the height of dc_1 divided by dp_4 area (a ratio) showed that this representation of relative canine height explained only 22.5% of the variance. In addition, there are a number of taxa in which mesial cristids are equally developed on deciduous and adult female canines (for example, *Pan* and *Gorilla*), even though the deciduous canines are much shorter than those of the adult females.

All of these phenomena support rejection of the simple allometry hypothesis. Variation in the size of the mesial cristid is a function of more than a simple allometric trajectory.

Another important reason for rejecting the hypothesis that the mesial cristid is a simple allometric phenomenon related to canine projection or height is that, proximately, its development is probably, in part, a function of the influence of genes of the *incisor* morphogenetic field. Thus, for example, in early hominids, all specimens retaining both I_2 and C_1 show that the mesial half of C_1 very closely resembles (frequently in minute detail) the homologous surface on I_2. This indicates that the ontogenetic origin of the mesial cristid is not simply a function of genes in the canine morphogenetic field that influence crown height. And canine reduction, which probably is related ontogenetically to a weakening of the canine's morphogenetic field, does not automatically result in an opportunity for genes in the incisor morphogenetic field to influence the mesial surface of C_1. Some taxa with very small or reduced canines (for example, *Alouatta* and *Pan paniscus*) may have poorly developed mesial cristids (and they lack the other traits associated with incisal usage noted below).[2] This indicates that an increase in the influence of genes of the incisor morphogenetic field on the mesial surface of the mandibular canine depends (at least) on both the weakening of the canine's morphogenetic field *and natural selection related to incisal usage.* For these reasons, in fossil and recent humans the mesial cristid is not "well explained as a non-selected growth phenomenon" (Plavcan and Kelley, 1996).

In addition to a rejection of the assertion that the mesial cristid is a function of simple canine allometry, there are also ample data for anthropoids in general supporting rejection of the assertion that it is a *non-selected* phenomenon.

[1]The exceptions are *Adapis parisiensis*, *Callicebus*, and *Australopithecus/Homo.*

[2]*Alouatta* is a folivore and folivorous species have small incisors (they need less incisal preparation of food) and smaller mesial cristids, and in *P. paniscus* the greatly enlarged central incisors indicate that the primary locus of incisal activity has shifted to the median plane, thus diminishing the need for an incisal contribution from the mandibular canine.

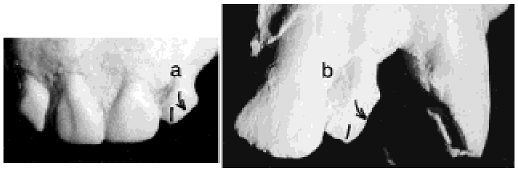

Fig. 1. Black lines on I^2s of *Saimiri* (**a**) and a Miocene hominoid (**b**) are positioned at the dividing point between their large distal moieties (curved arrows pointing) and much smaller mesial moieties. These surfaces occlude, respectively, with the mesial cristid of C_1 and the distal surface of I_2. If the mesial cristid has no adaptive significance, then most of the I^2 crown has been sacrificed to occlude with a nonselected phenomenon. Because this is very unlikely in these taxa, as well as most other anthropoids since the Eocene, the nonselected hypothesis is falsified.

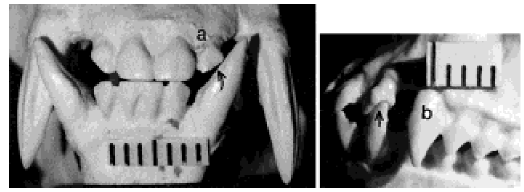

Fig. 2. Is the occlusal relationship (see arrows) between the C_1 mesial cristid and the distal moiety of I^2 identical in conspecific males and females because the C_1s of both sexes contact the distal moiety at about the same frequency? The illustrated specimens (male and female, respectively, **a** and **b**) show that the *frequency of contact* should not be equated with the *form of contact*. In most anthropoid species, females exhibit an incisor-like occlusion that is absent in conspecific males (also see Greenfield, 1996b).

If the mesial cristid is a non-selected growth phenomenon, then the maxillary lateral incisor's relationship to it should be nil or nonexistent. This is not so. Variation in I^2 morphology very consistently covaries with mesial cristid size in female anthropoids and the morphology and occlusal relationships between the two teeth have covaried and coevolved since the Eocene (Greenfield, 1996a, and in preparation). More importantly, in most Eocene–Recent anthropoids, the distal moiety of I^2, the occlusal partner for the C_1 mesial cristid, has been of equal or greater size than the mesial moiety of I^2 that occludes with the distal portion of I_2. In *Saimiri* (Fig. 1), for example, one can only conclude that selection for an occlusal relationship with the mesial cristid of the female C_1 has caused the distal moiety of I^2 to be more than twice the size of the mesial moiety—it is unlikely that most of the occlusal surface of I^2 would be sacrificed to interact with a non-selected growth phenomenon (the mesial cristid of C_1). *Saimiri* is not an isolated instance. Adapids, probable anthropoid ancestors, and most anthropoids from the L. Eocene–Miocene (Greenfield, 1996a) have I^2s with distal moieties that are equal to or larger than their mesial moieties. Most anthropoid I^2s also possess an occlusal concavity built specifically for the mesial cristid of female C_1s. On the other hand, when the distal moieties of female anthropoid I^2s are small and/or when there is no occlusal concavity, the mesial cristid is poorly expressed (as, for example, in folivores generally). This variation in the condition of the distal moiety cannot be explained as a simple consequence of C_1 proximity, as the vestigial mesial cristids of conspecific male canines are equally proximate to the distal moiety of I^2 and these have no functional occlusal relationship or coevolution with each other (Greenfield, 1996b).[3] All of these observations indicate that the mesial cristid on female C_1s is a naturally selected phenomenon related to incisal occlusion with I^2. In sum, contra Plavcan and Kelley, the mesial cristid in anthropoids generally, and in humans specifically, is not "well explained as a non-selected growth phenomenon."

Plavcan's and Kelley's (1996) quantitative assessment of the occlusal interaction between the mesial cristid and the lateral incisor is also flawed. According to these authors, the mesial surfaces of the mandibular canines of males and females contact I^2 at about the same frequency (almost 90%) and conclude that there is no difference between the sexes. Even if these data are correct, *frequencies of contact* cannot be used as evidence for no difference in the *form of contact*. Thus, for example, as shown in Figure 2, based on Plavcan's and Kelley's argument one would have to conclude that the C_1/I^2 occlusal relationship is identical in these male and female *Saimiri* specimens because the C_1s of both sexes contact I^2—it is clearly not identical. In the female there is

[3]The condition of male I^2s is identical to females, yet they have no well-developed mesial cristids—this is an instance of correlated response (see detailed discussion in Greenfield, 1996b)

a functional incisal occlusal relationship; in the male the contact is nonfunctional with respect to incisor-like occlusion. Clearly, a quantitative assessment cannot be used to assess whether the form of contact is different. Across all taxa, it is inappropriate to equate the morphology of this interaction with the simple frequency of contact. They are not equivalent.

Canines and incisors: Overlap in form and function

According to the dual selection hypothesis, although not optimally designed, adult female and deciduous canines look sufficiently like incisors to function as incisors. In contrast, although Plavcan and Kelley (1996) do not state what an incisor looks like, they appear to be saying that any tooth that is not flat-surfaced (vs. pointed) and spatulate cannot be an incisor or have incisal functions: for example (p. 384) "maxillary canine teeth in females do not look like incisors."

The variation in canine and incisor form and function among anthropoids do not support this viewpoint; the morphologies and uses of canines and incisors overlap extensively. To show this is true for the maxilla, in Figure 3 I have pictured maxillary teeth from several dietarily diverse taxa within the suborder (*Callithrix, Alouatta, Macaca,* and *Presbytis*) that, according to Plavcan and Kelley (1996), could not function like incisors because they don't look like incisors. Yet, all are maxillary lateral incisors. The more interesting point is that they do not look significantly different from most female or deciduous maxillary *canines.* Indeed, in many nonanthropoids like *Tarsius,* omomyids, and plesiadipiformes, incisors are conical and pointed. In anthropoids, low-crowned deciduous maxillary canines and the maxillary canines of adult females fall within the range of maxillary incisor form.

With respect to mandibular canines, there are numerous examples showing that projecting conical teeth, even those with poorly developed mesial cristids, are used for incisal functions. Several of these, including *Cebuella,* pithecines, and humans are discussed in detail by Plavcan and Kelley (1996). A fourth case (*Cebus*) is not discussed by

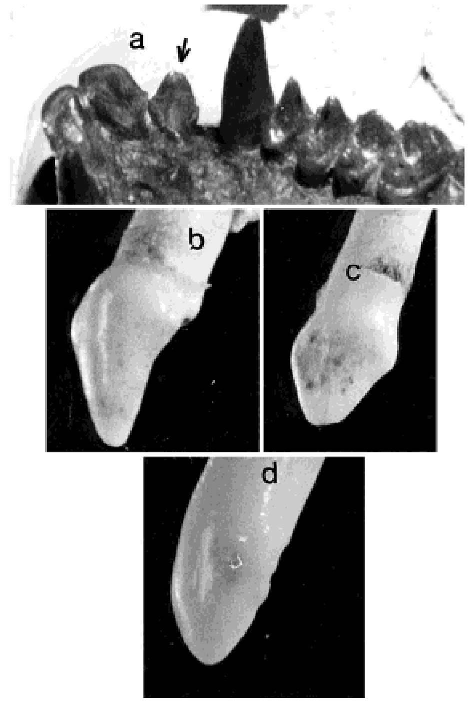

Fig. 3. Pictured are caniniform teeth from dietarily diverse taxa (*Callithrix* (**a;** arrow pointing), *Presbytis* (**b**), *Alouatta* (**c;** apex of crown is worn), *Macaca* (**d**)). All are I^2s. These examples show that morphological variation in anthropoid maxillary incisors includes the morphologies of anthropoid deciduous and female maxillary canines and that caniniform teeth can have incisal functions. The idea that incisors are flat crowned and spatulate was used to reject the assertion that canine-like teeth can have incisal functions. Known incisal uses of caniniform mandibular canines (in marmosets, pithecines, *Cebus,* and humans) also shows that teeth do not have to be flat and spatulate to have incisal functions.

them, although here too recent observations (Anapol and Lee, 1994) have shown that large and projecting conical canines in both sexes are being used for incisal functions.

Plavcan and Kelley (1996) do acknowledge that *Cebuella* is an exception where individuals habitually use their canines as incisors in food gathering. Presumably they would conclude that this is also true for the other genus of marmoset, *Callithrix,* which has the same morphology, albeit at a slightly larger size than *Cebuella.* They further state that the "canines of *Cebuella* are clearly altered into incisor-like teeth."

The anterior teeth of a *Callithrix* specimen (a *Cebuella* specimen would be the same) are illustrated in Figure 4. This lat-

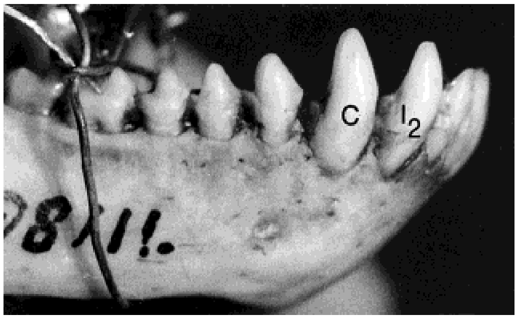

Fig. 4. A lateral view of a marmoset (a group that includes two size variants—*Cebuella* and *Callithrix*) shows that the canine and lateral incisors are similar in form to each other and that they both look more like conical projecting canines. Both are used as incisors and form a scraping battery. This, however, contradicts the view that anterior teeth must be flat and spatulate to have incisal functions and the logical consequence of that view that canine-like teeth cannot have incisal functions.

eral view shows that it is not so much that the projecting and conical marmoset canine (that has a scraping apex) has become altered to look like the incisor but, rather, the lateral incisor which has been modified to look more like the canine. This caniniform incisor, which forms a scraping battery with C_1 (an incisal function), also looks caniniform from the occlusal view, which shows that both teeth are aligned like canines and that their shapes, as measured by length/breadth proportions (Table 2), are also similar. In most taxa, mandibular canine length exceeds breadth but the opposite occurs in the lateral incisor. However, in *Cebuella* and *Callithrix* the lateral incisor is like the canine with length greatly exceeding the breadth.

This example supports several points: the morphology of both teeth is more caniniform than incisiform; that teeth that are tall, projecting, and conical can have incisal functions, and that, in some cases, conical projecting tusks provide better incisal functions than shorter spatulate teeth. The conditions in *Cebuella* and *Callithrix* are also important because they show that human mandibular canines, with shorter crowns and well-developed mesial cristids, are far more like incisors than marmoset mandibular canines (compare Fig. 4 with human canines in Fig. 5).

TABLE 2. Shape measurements for I_2 and C_1 in ceboids*

	I_2	C_1
Cebuella pygmaea	1.75	1.80
Callithrix argentata	1.69	1.53
Cebus apella	0.75	1.26
Saimiri sciureus	0.74	1.10
Ateles geoffroyi	0.83	1.21
Saguinus mystax	1.00	1.26
Lagothrix lagotricha	0.84	1.27
Alouatta palliata	0.79	1.24
Callicebus moloch	0.69	1.58

* Mesiodistal length/buccolingual breadth.

Plavcan's and Kelley's analysis of pithecine canines also illustrates a problematic reading of morphology. Because pithecine canines are tall, projecting, and pointed, they must argue that these teeth are doing something that incisors cannot do. Consequently, they state that "pithecines are clearly using their canines to do what their incisors cannot do (open hard objects), demonstrating that use of the canines for food procurement does not necessarily mean that the canines will function as incisors or look like incisors."

This is a self-contradictory statement, as food procurement is an incisal function, which these authors also agree is true (see Plavcan and Kelley, 1996:386, on human canines). Further, teeth with incisal functions (as demonstrated by the canines of *Cebuella*, *Callithrix*, *Cebus*, and humans, and the I^2s of taxa noted above) can be caniniform. However, more importantly, a more complete reading of morphology shows that pithecines have some of the most peculiar maxillary and mandibular incisors among extant anthropoids. In particular, they are narrow and extremely procumbent—a morphology which suggests that they do not do much vertical compression. Rather, they have evolved into a specialized, bilaterally compressed gouge for removing seeds (Anapol and Lee, 1994). Given the known dietary uses and morphology of the canines, it is reasonable to hypothesize that the canines have assumed the vertical compression functions of the incisors. This indicates that the canines are not only doing what the incisors cannot do, but also have taken over some of the functions that incisors ordinarily do. And the canines have

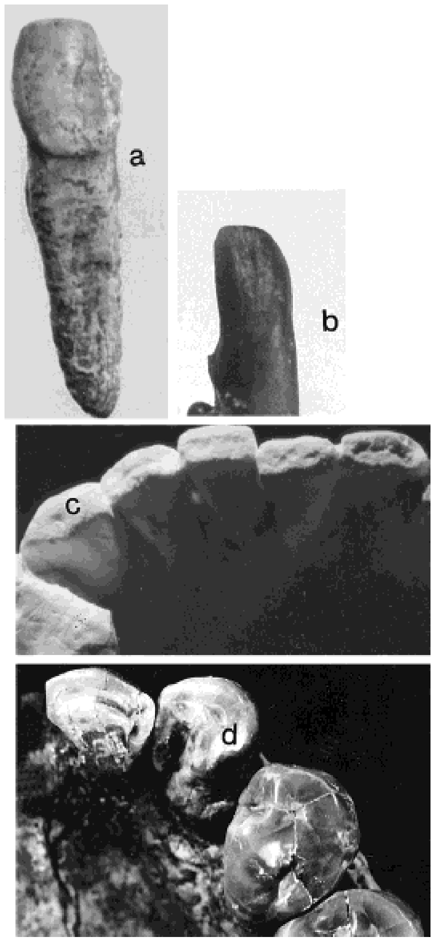

Fig. 5. Specimens of *Australopithecus* (**a, c,** and **d**) and an adapid (**b**) show that unworn (b) and worn canine teeth (a, c, and d) can look like flat and spatulate incisors and can function like incisors. The form and function of canines and incisors overlap extensively. Also note the numerous incisor-like traits in early humans that Plavcan and Kelley maintain are accidents of crown reduction having nothing to do with natural (incisal) selection for these traits: an increase in the size of the mesial cristid, marked convergence in morphology between I_2 and C_1, alignment of C_1 with the curved tooth row, closing of the diastemata, lingual movement of the C_1 crown, and universal tip-to-tip occlusion and blunting wear between C_1 and C^1 and I^2.

done so even though they are not short and spatulate.

With respect to human canines, Plavcan and Kelley acknowledge that they "function in concert with the incisors for food procurement." They do not seem to recognize, however, that this contradicts their assertion that teeth with incisal functions have to be short and spatulate and their statement that "when canines function as incisors, they are modified by selection to look like incisors in both sexes" (for example, as they claim is the case in *Cebuella*—see above).

Plavcan and Kelley (1996) try to make the argument that incisal usage played no part in human canine evolution and that their known incisal uses are an accidental byproduct of canine reduction. Yet, the earliest human canines found to date show, in addition to their still large but reducing size and declining dimorphism, a marked increase in the size of the mesial cristid (as a consequence of the expanding influence of the incisal morphogenetic field), a strong convergence in morphology of C_1 and I_2, realignment of C_1 with the curved row of incisors, a closing of both diastemata resulting in a lingual movement of both crowns that better allows tip-to-tip occlusion, and blunting wear that occurs on most, if not all, crown tips (see Fig. 5 here and Figs. 16 and 18 of Greenfield, 1992a). Even the *A. anamensis* type specimen (KNM-KP 29281), dated to 4.1 Myr and pictured by Leakey et al. (1995), clearly shows all of these features. These early changes, which all favor better use of the canines for incisal functions (that human canines are known to perform), accompany, rather than follow, crown reduction. In fact, most of the morphological changes have been accomplished while only some of the reduction in size has been achieved. And, *none of these changes can be explained as consequences of a simple allometric trajectory of canine height reduction*. Thus, rather than happy accidents, all of these changes are far more likely to be consequences of natural selection for incisal usage and represent adaptations, not exaptations.

In sum, anthropoid canines and incisors overlap extensively in form and function and anthropoid deciduous canines, adult female canines, and fossil and recent human canines easily fall within the incisor range and are less caniniform than marmoset, pithecine, and *Cebus* canines, all of which are known to have incisal functions.

Deciduous and male canine form

According to the dual selection hypothesis, selection for incisal usage of male ca-

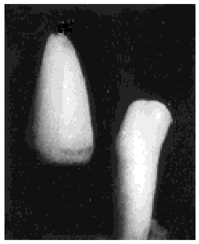

Fig. 6. A single specimen of a male *Macaca* shows that there are two sizes and morphs, and most likely two different uses, of canine teeth—one short and spatulate and the other tall and conical (⅓ of the unerupted crown is shown). This pattern is found in the vast majority of anthropoid species. See text for more discussion of other sources of intraspecies variation.

nines also exists even though the size and morphology of their canines do not reflect this selection. However, in their discussion of male canines, Plavcan and Kelley (1996) imply that an orthogenetic argument has been used to argue for incisal selection in males. They state that "if male canines are not used as incisors, and in fact cannot be used as incisors, how can selection operate for this consequence unless it is somehow prescient of future use?"

The answer to this question has already been discussed (Greenfield, 1992a,b). Nowhere in their discourse do they mention the significance of deciduous canines in the dual selection argument. The deciduous precursors of almost all anthropoid male canines have better-developed mesial cristids and lower crowns than females. Figure 6 shows a male macaque with an incisor-like dc_1 and the top third of the same individual's tall and conical permanent successor. This dc_1 is certainly flatter and more spatulate than any of the incisors pictured in Figures 3, 4, and 5. And it is not an exceptional specimen. The deciduous canines of the great majority of anthropoids have comparable traits (Greenfield, 1992b), indicating that there is incisal selection at the canine position in males and females. One should presume that the same selection exists at this tooth position in the adults (of both sexes) because similar or identical forms of selection exist for all the other tooth positions between adult and deciduous teeth. The only difference for this tooth position is that there are *competing* forms of selection in adult males that favor mutually exclusive morphologies and hierarchically, weapon selection outweighs incisal selection. This is not unusual, as many traits evolve with competing forms of selection present. However, if a structure cannot be compromised (hybridized or generalized) to perform adequately to satisfy all forms of selection and to generate the highest level of fitness, the most intensely selected specialized form will win out and the structure will not reflect the less intense forms of selection. This lack of reflection does not mean that the weaker form of selection is absent. Thus, for example, bipedalism evolved, and has been maintained by strong stabilizing selection, despite the slowness, lack of agility, and numerous anatomical disadvantages that accompany it (Straus, 1962).

Related to this same question, Plavcan and Kelley (p. 386) correctly state that "in order for selection to modify a structure for a particular function, there must be some variability in function and morphology with an effect on individual fitness on which selection can operate." In this instance, virtually all anthropoids have three different forms and sizes (and uses) of canines, with high levels of phenotypic and (probably) genetic variation, that are likely to be genetically linked to each other and with varying genes that regulate the strength of the morphogenetic field of the incisors. In addition, all adult males already carry the genes necessary to make their canines shorter and more incisiform as evidenced by their deciduous canines, and these same individuals have varying uses of the teeth at the canine position. This, and the two conditions in females, constitutes a pool of variation in size, form, and function more than sufficient to make possible the natural selection needed in the dual selection hypothesis. In fact, intraspecies variation in the size, form, and function of this tooth is greater than for any other tooth in the dentition.

CONCLUSIONS

The data presented show that female canine tip wear is common and that it occurs at a higher frequency than in conspecific males in both jaws.

Plavcan's and Kelley's analysis of the dual selection hypothesis (1996) reflects their strong adherence to several null hypotheses. These include the hypotheses that structures are optimally designed and are a consequence of natural selection. Since female canines are not optimally designed for incisal usage, Plavcan and Kelley believe that they cannot have incisal functions. For most traits, I agree with Plavcan and Kelley that these should be the null hypotheses. However, for traits that show sexual dimorphism the null hypothesis should be that they are affected by correlated response. Less-than-optimal design in one or both sexes and a complex natural selection process are expected.

In a recent paper (Greenfield, 1996a) three aspects of the anthropoid C/P complex that are best explained by a correlated response model (that includes the effects of selection) have been analyzed. According to that analysis and model, when selection for weapon use is absent and when the compromising effects of correlated response are removed, the result is canines that fall within the range of variation for incisal size and form. There are examples of these in virtually all anthropoids of both sexes—deciduous canines. Fossil and recent human canines, known to have incisal uses, have converged in size and form with anthropoid deciduous canines. This, and the evolutionary changes in size and form that enhanced incisal usage of canines in the earliest known species in the human lineage, show that human canine evolution can be explained as a consequence of their diminished need as weapons and because of the preexisting selection for their use as incisors.

ACKNOWLEDGMENTS

I thank the Mammalogy Department of the American Museum of Natural History for access to extant primate materials and Muriel Kirkpatrick (Anthropology Department/Temple) for help with the photographic work. I also thank Dr. William Kimbel for the photograph of Al 400-1a. Thanks, also, to that the editor of AJPA and a reviewer for critical comments.

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